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# Thermal ecology of the South American leaf-toed gecko *Phyllodactylus gerrhopygus* (Wiegmann, 1834) (Gekkota, Phyllodactylidae) in northern Chile

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## Abstract

Body temperature is fundamental for the ecology of ectotherms due to its direct effect on their fitness. The thermoregulation of small reptiles involves a regulatory process that depends on morphophysiological and behavioural adjustments, along with environmental thermal characteristics, to maintain as close as possible to their optimum temperature. In this study, we evaluated the thermoregulation capacity of *Phyllodactylus gerrhopygus*, a relatively small and crepuscular-nocturnal gecko. Specifically, the aims of the present work were: 1) to determine if this species behaves as a thermoregulator or thermoconformer species, 2) to examine if the preferred body temperatures ($T_{pref}$) vary during the hours of potential thermoregulation and 3) if there are differences in daily patterns of $T_{pref}$ and thermoregulation between juveniles and adults. In the field, we recorded the $T_b$ of geckos and the substrate ($T_s$) and air ($T_a$) temperatures from their refuges. In the laboratory, we evaluated $T_{pref}$ by recording the temperature geckos selected in a thermal gradient at different times of the day. We found a positive association between $T_b$ and $T_s$. The positive correlation between $T_b$ and refuge temperature suggests that *P. gerrhopygus* is a thigmothermic and thermoconformer species. Both juveniles and adults select similar temperatures and neither of them thermoregulates. The $T_{pref}$ was significantly higher during the evening (32.23 ± 5.91 °C) than the morning period (25.2 ± 9.02 °C). We did not find differences between juveniles and adults. Our results are similar to those found in other phylogenetically close lizards, suggesting a strong phylogenetic inertia in thermal preferences.

## Key Words

desert climate, ectotherms, lizards, micro-habitat, thermoregulation

## Introduction

Body temperature ($T_b$) plays a crucial role in the ecology of ectotherms because it directly influences their fitness (Huey and Berrigan 2001). The temperature affects various activities, such as foraging, movement and reproduction in these organisms (Peterson et al. 1993; Angilletta 2009). In this regard, thermoregulation is crucial for maintaining body temperature within appropriate ranges and preventing extreme temperatures. For small reptiles like other ectotherms, thermoregulation involves a combination of physiological and behavioural adaptations, enabling animals to achieve a $T_b$ that maximises their physiological functions or overall performance (Cowles and Bogert 1944; Avery 1982; Angilletta et al. 1999; Aguilar and Cruz 2010; Lara-Resendiz et al. 2013; Lap-

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wong et al. 2020; Mouadi et al. 2020). This process of thermoregulation is influenced by several factors related to the organisms' activity periods, which differ between their active and inactive times (Angilletta et al. 1999).

Small nocturnal reptiles depend on their diurnal microhabitat for shelter and as sites for thermoregulation (Kerney and Predavec 2000; Webb and Shine 2000). For example, during the day, they maintain their $T_b$ within a selected interval of preferred temperature ($T_{pref}$) to carry out their physiological temperature-dependent processes, such as digestion, growth and reproduction (Angilletta and Werner 1998; Aguilar and Cruz 2010; Lara-Resendiz et al. 2013). On the other hand, during the night, the thermal quality of the environment decreases and the opportunities to achieve appropriate temperature for foraging, locomotion, socialization, escape or defence from predators are limited (Kearney and Predavec 2000; Aguilar and Cruz 2010). At night, there are decreased opportunities for thermoregulation, but social activities in this period increase the risk of injury and predation and there is higher energy expenditure (Lara-Resendiz et al. 2013). However, the daytime period of 'inactivity' could be thermally advantageous since various reptiles can actively control $T_b$ more accurately inside their shelter than when they are out and active, highlighting the importance of microhabitat selection (Cowles and Bogert 1944; Huey et al. 1989; Lara-Resendiz et al. 2013).

$T_b$ and $T_{pref}$ are frequently used to study the thermal ecology of small ectotherms, especially in lizards (Angilletta et al. 1999; Huey and Berrigan 2001; Aguilar and Cruz 2010; Lara-Resendiz et al. 2013). The $T_{pref}$ can be obtained by placing an animal in a linear temperature gradient selected by organisms in laboratory conditions (Huey and Berrigan 2001; Alfaro et al. 2013; Taucare-Ríos et al. 2020) and it is an environment that is independent of the ecological cost (Hertz et al. 1993). In lizards, such as geckos, $T_{pref}$ can be influenced by intrinsic (e.g. sex, age and body condition of individuals) and extrinsic factors (environmental conditions) (Angilletta et al. 1999; Aguilar and Cruz 2010; Lapwong et al. 2020; Mouadi et al. 2020). Some authors have suggested that preferred body temperature, being part of the thermal niche, can be considered a phylogenetically conserved trait and/or, in some cases, has high phenotypic flexibility to environmental changes (Labra et al. 2009; Clusella-Trullas et al. 2014; Giacometti et al. 2024).

The thermal quality of the habitat selected by geckos depends on the difference between the available environmental temperatures and their $T_{pref}$ (Angilletta et al. 1999; Huey and Berrigan 2001; Blouin-Demers and Nadeau 2005; Tan and Schwanz 2015). Night temperatures may influence thermoregulatory strategies if, for example, warm temperatures create numerous microhabitats near the preferred temperature or if cool temperatures limit the availability of microhabitats near the preferred temperature (Tan and Schwanz 2015).

The South American Leaf-toed Gecko *Phyllodactylus gerrhopygus* (Wiegmann, 1834) is a relatively small gecko (Snout to Vent Length, SVL ≈ 50 mm) that is primarily crepuscular and nocturnal. It is endemic to the desert regions of Chile and Peru (Aguilar et al. 2015; Ruiz de Gamboa 2016) and is currently listed as Least Concern (IUCN 2023). The ecology and behaviour of *P. gerrhopygus* remain largely unstudied. This gecko inhabits rocky and sandy coastal areas of deserts and even in human environments, they seek refuge during the day under rocks, logs or anthropogenic debris (Mella 2017). The species has a generalist and insectivorous diet and acts as an opportunistic predator, mainly preying on spiders, followed by beetles, insect larvae and solifuges (Pérez and Balta 2011). They remain active throughout the year, including winter (July-September), surviving in conditions with median air temperatures of around 13 °C at sea level and 7 °C at 3400 m above sea level (Kroll and Dixon 1972). However, there is little to no published information regarding its thermal ecology.

This study aimed to investigate the thermal biology of *P. gerrhopygus*, specifically examining the interplay of intrinsic and extrinsic factors influencing its preferred body temperature and elucidating the thermoregulatory strategies employed by the species in its natural habitat. We addressed the following questions: 1) What is the effect of intrinsic (age class, body size) and extrinsic factors (time of day) on field $T_b$ and preferred laboratory temperatures? 2) What thermoregulatory strategy does *P. gerrhopygus* employ to maintain its field $T_b$ — thigmothermy or heliothermy?

# Material and methods

## Study area and fieldwork

Individuals were collected at the Huayquique Campus, near Huayquique Beach (20°16'17"S, 70°7'51"W) in the spring of 2023, Iquique, Tarapacá Region, Atacama Desert (Fig. 1). This area is characterised by the presence of dunes, rocks and limited vegetation. Spring and summer are hot, arid and partly cloudy, while abundant clouds and low thermal oscillation characterise winter (McKay et al. 2003; Luebert and Pliscoff 2006).

The lizards were caught manually under rocks and debris for a total of four hours. The sample size for each age group was balanced across different periods of the day. We recorded body temperature ($T_b$) (dorsal skin temperature) of geckos and the substrate ($T_s$) and air ($T_a$) temperatures from their refuges using a non-invasive infrared thermometer (EXTECH Instrument, model IR267; IR accuracy: ± 0.2 °C with 12:1 as distance-to-spot ratio (DS). When a gecko was located, the $T_b$ was measured from 20 cm away at the dorsal skin during the first 5 seconds after the specimen was found. Recently studies have reported that measuring dorsal skin temperature with an infrared thermometer provides a good representation of cloacal temperature in relatively small lizards, such as geckos, thereby validating this methodology (Hare et al. 2007; Carretero 2012; Bouazza et al. 2016; Mouadi et al. 2020). Substrate temperatures were measured by placing the thermometer against the substrate 5 cm above

**Figure 1.** Individual of the gecko *Phyllodactylus gerrhopygus* captured in Campus Huayquique, Iquique, Tarapacá Region, Chile (photo by Dyana Leiva). Scale bar: 20 mm.

the ground at the location where the lizard had first been observed. Air temperatures were recorded 5 cm above the substrate at the place of first sighting. This model (IR267) can simultaneously measure air temperature (mode A), substrate (mode S) and body temperature (mode O). Individuals were placed in plastic containers (250 $cm^3$) containing a small piece of wet cotton. Lizards were weighed (± 0.001 g) and measured (SVL: ± 0.01 mm). SVL was measured using a clear plastic ruler and body mass was measured using a precise analytical scale (Hays et al. 2019). Their SVL determined the age-class of the captured individuals as: juveniles, if their SVL was ≤ 50 mm and adults, if their SVL was > 50 mm (Mella 2017).

## Field body temperatures and thermoregulation

We evaluated the thermoregulatory precision of the species using the index db suggested by Hertz et al. (1993). The index db indicates the extent to which geckos experience $T_b$ outside of $T_{pref}$ and was calculated as the mean absolute deviation between $T_b$ and the extremes of the $T_{pref}$ range. Larger values indicate less accurate thermoregulation or thermoconformism. Furthermore, if the relationship between $T_b$ and $T_a$ *i*s higher than the relationship between $T_b$ and $T_s$, it is assumed that there is a tendency towards heliothermic behaviour, which means it captures heat directly from solar radiation. If the opposite occurs, the strategy is thigmothermy, where the organism gains heat through direct contact with the substrate (conduction) (Cardona-Botero et al. 2019).

## Laboratory preferred temperatures

Individuals were kept in a room for two weeks, subject to natural variations in room temperature (25.5 ± 2.5 °C, mean ± standard deviation) and relative humidity (62 ± 3.1%). They were exposed to a 12L:12D photoperiod with natural light conditions during the first week of laboratory acclimatisation and the second week of experiments. Geckos were fed with live spiders (*Loxosceles laeta*) *ad libitum* and were fasted for 3 days before measurement of $T_{pref}$. We consider that these are sufficient days of fasting to minimise the impact of feeding and digestion on the selected body temperature (Dayananda and Webb 2020). Then, each one was placed on a horizontal temperature gradient between 10 °C and 40 °C, built in a rectangular glass container measuring 0.5 × 0.1 × 0.1 m (length × width × height) and halfway submerged in water in a thermoregulated chamber measuring 0.5 × 0.2 × 0.2 m with infrared lamps suspended above the gradient. This chamber had a thermoregulated heater (100 W titanium heater) on one side and a cold point on the other (cooling gels), generating a thermal gradient between the endpoints. The floor of the gradient was covered with a thin layer of sand. Refuges were provided along the thermal gradient (Mouadi et al. 2021). Before the experiments began, the thermal gradient was calibrated using a type-K thermocouple installed at 10 cm intervals.

Individuals were exposed to a thermal gradient for 1 hour at two different times of day: morning and evening. Individuals were randomly deposited in the chamber and acclimatised in the gradient for one hour. Then, we recorded the temperature (represented by dorsal skin temperature) that the gecko selected in the gradient every 5 minutes for 1 hour using an infrared thermometer (EXTECH Instrument, model IR267; IR accuracy: ± 0.2 °C). This process was repeated once in the morning, between 10:30 h and 11:30 h and once during the evening, between 19:30 h and 20:30 h. The measurement accuracy of the infrared thermometer was previously studied by comparing the measurements of substrate temperatures obtained with this device and those obtained with a copper thermocouple. We compared the temperature obtained by the infrared thermometer and the K-type thermocouple and found no significant differences (t-test = 0.71, $p = 0.49$).

## Analysis and statistics

We measured $T_{pref}$ in nine adults and 11 juveniles. We represented $T_{pref}$ by a frequency histogram of the chosen temperatures. The histogram was obtained using the individual values of the measurements taken every 5 minutes during the two times of day for the 20 individuals studied. The data fit the assumptions of normality and homocedasticity (Shapiro-Wilk test and Levene's test, respectively). Therefore, we used repeated measures ANOVA to examine the effects of age class and time of day on the $T_{pref}$ of *P. gerrhopygus*, with $T_{pref}$ as the response variable and the

age class and the two experimental times as the factors ($\alpha = 0.05$). We calculated the mean $T_{pref}$ in the gradient and $T_{pref}$ lower and $T_{pref}$ upper as the 25th and 75th percentiles (preferred temperature range) (Hertz et al. 1993). We used Student's paired t-test to compare the temperatures obtained in the field and the laboratory ($T_a$ vs. $T_{pref}$, $T_s$ vs. $T_{pref}$, $T_b$ vs. $T_{pref}$). Relationships between $T_{pref}$ and body size (mass and SVL) and $T_b$ and $T_s$, $T_a$ were assessed using linear regression. All these analyses were conducted using the PAST software, Version 3.14 (Hammer et al. 2001). Data are presented as means ± SD.

## Results

We collected data from 20 individuals, comprising nine adults and 11 juveniles. The individuals had a body mass of 1.69 ± 0.72 g and measured 47.21 ± 7.5 mm of SVL. The field $T_b$ was 26.1 ± 4.05 °C and the $T_s$ was 25.81 ± 5.13 °C (Table 1). No differences were found between adults and juveniles in field $T_b$ (t-test, $t_{18} = 0.79$, $p = 0.43$). We found a strong positive association between $T_b$ and $T_s$ ($r = 0.88$, $p < 0.05$) and a moderate association between $T_b$ and $T_a$ ($r = 0.44$, $p < 0.05$). We found that mean db was 5.82 ± 4.3, showing low accuracy in thermoregulation (thermoconformism), with a low difference between juveniles (6.7) and adults (4.2). A linear regression of $T_{pref}$ versus SVL for all animals collected did not indicate a significant relationship ($p = 0.16$, $F_{1,18} = 0.04$, $R^2 = 0.002$, slope = -0.004). No linear relationship was found between body mass and $T_{pref}$ either ($p = 0.15$, $F_{1,18} = 0.035$, $R^2 = 0.001$, slope = -0.39). The results show that *P. gerrhopygus* is a thigmothermic species with a significant relationship between $T_b$ and $T_s$ ($p < 0.05$, $F_{1,18} = 64.63$, $R^2 = 0.78$, slope = 0.69) (Fig. 2) and a significant relationship between $T_b$ and $T_a$ ($p < 0.05$, $F_{1,18} = 4.9$, $R^2 = 0.21$, slope = 0.85). No differences were found between $T_b$ and $T_{pref}$ (paired t-test, $t_{18} = 1.45$, $p = 0.15$) or $T_s$ and $T_{pref}$ (paired t-test, $t_{18} = 1.5$, $p = 0.14$). Still, there is a significant difference between $T_a$ and $T_{pref}$ (paired t-test, $t_{18} = 2.36$, $p = 0.02$).

**Table 1.** Average morphometric and body temperatures for juveniles and adults.

| Variables | Juveniles (n = 11) | Adults (n = 9) |
|---|---|---|
| Mass (g) | 1.36 ± 0.58 | 2.05 ± 0.69 |
| SVL (mm) | 45.22 ± 7.32 | 49.96 ± 7.02 |
| $T_b$ | 25.44 ± 3.77 | 26.91 ± 4.46 |
| $T_s$ | 25.29 ± 5.12 | 26.44 ± 5.68 |
| $T_{pref}$ | 28.83 ± 7.80 | 28.23 ± 4.52 |

The mean $T_{pref}$ in the thermal gradient was 28.63 ± 9.41 °C (range = 9.2–41 °C; n = 20) with $T_{pref}$ 25 of 25.55 °C and the $T_{pref}$ 75 of 35.77 °C. The frequency histogram showed a precise bimodality distribution in the selected temperatures with differences between morning and evening period (Fig. 3). The $T_{pref}$ was significantly higher during the evening (32.23 ± 5.91 °C) than the morning period (25.2 ± 9.02 °C) (two-way repeated measures ANOVA, $F_{1, 17} = 18.36$, $p = 0.0005$) (Fig. 4). We did not find differences between adults and juveniles (two-way repeated measures ANOVA, $F_{1,17} = 0.14$, $p = 0.71$).

## Discussion

Both field $T_b$ and $T_{pref}$ obtained in the laboratory showed a preference for warm temperatures. We found that both $T_b$ and $T_{pref}$ were not influenced by intrinsic factors such as age class or body size, but were affected by changes in the time of day. Geckos had lower body temperatures during the morning and increased them during the evening.

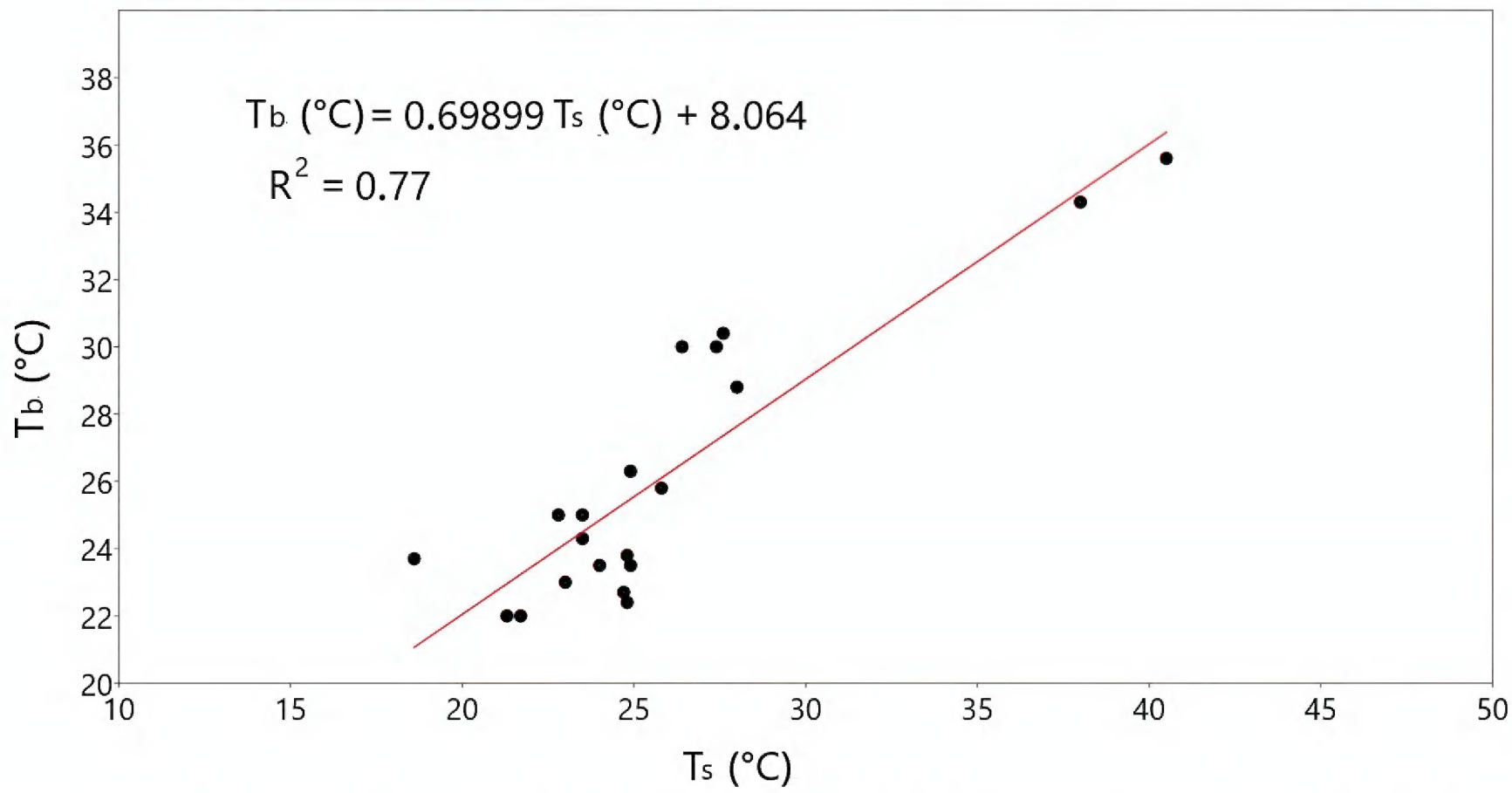


**Figure 2.** Linear regression analysis between body temperature ($T_b$) of *Phyllodactylus gerrhopygus* and substrate temperature ($T_s$). The line represents the best fit for the scatter plot data.

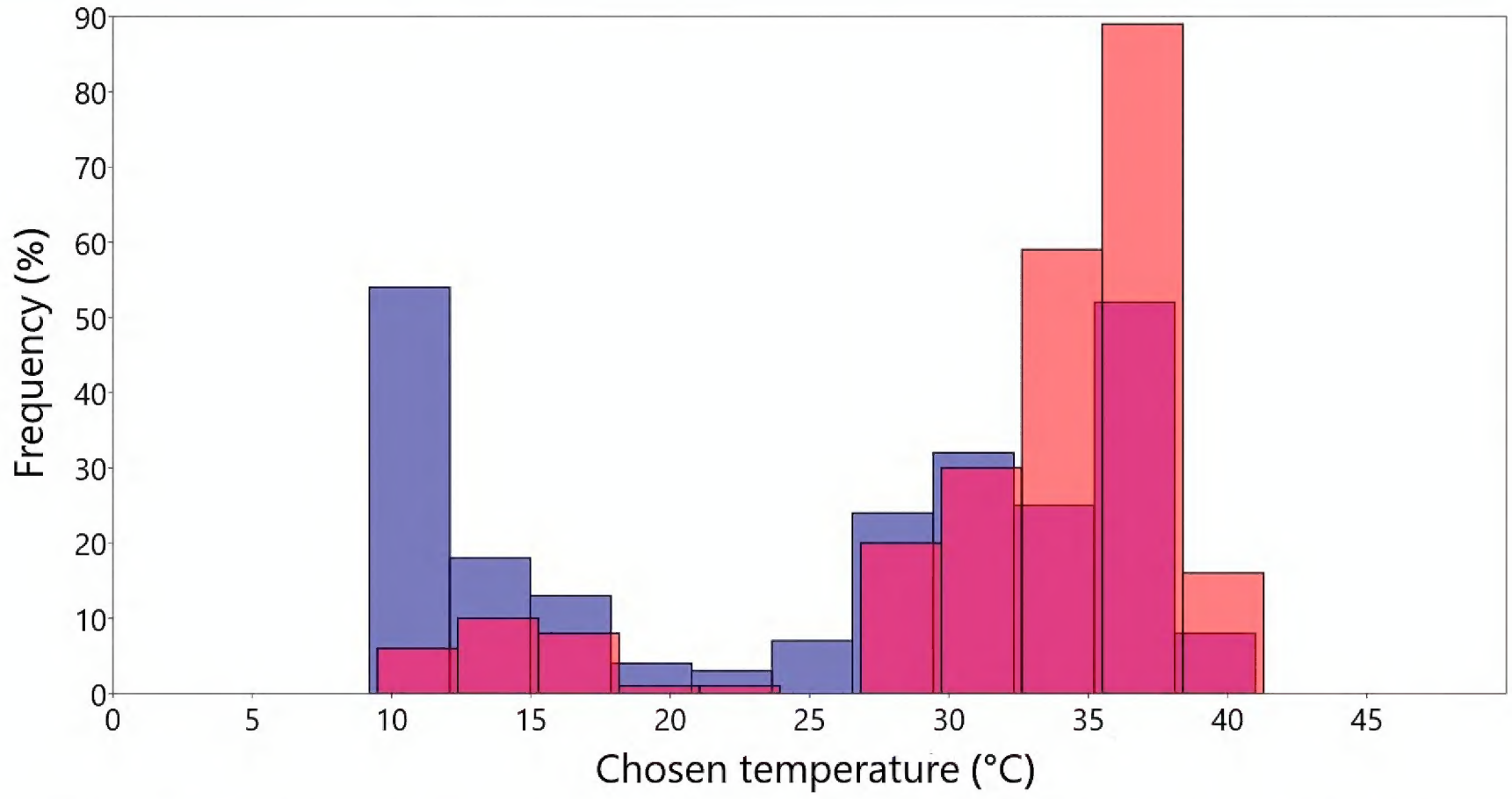


**Figure 3.** Frequency histogram of preferred temperatures ($T_{pref}$) (percentage of all recordings) for *Phyllodactylus gerrhopygus*. Blue: morning period; Red: evening period.

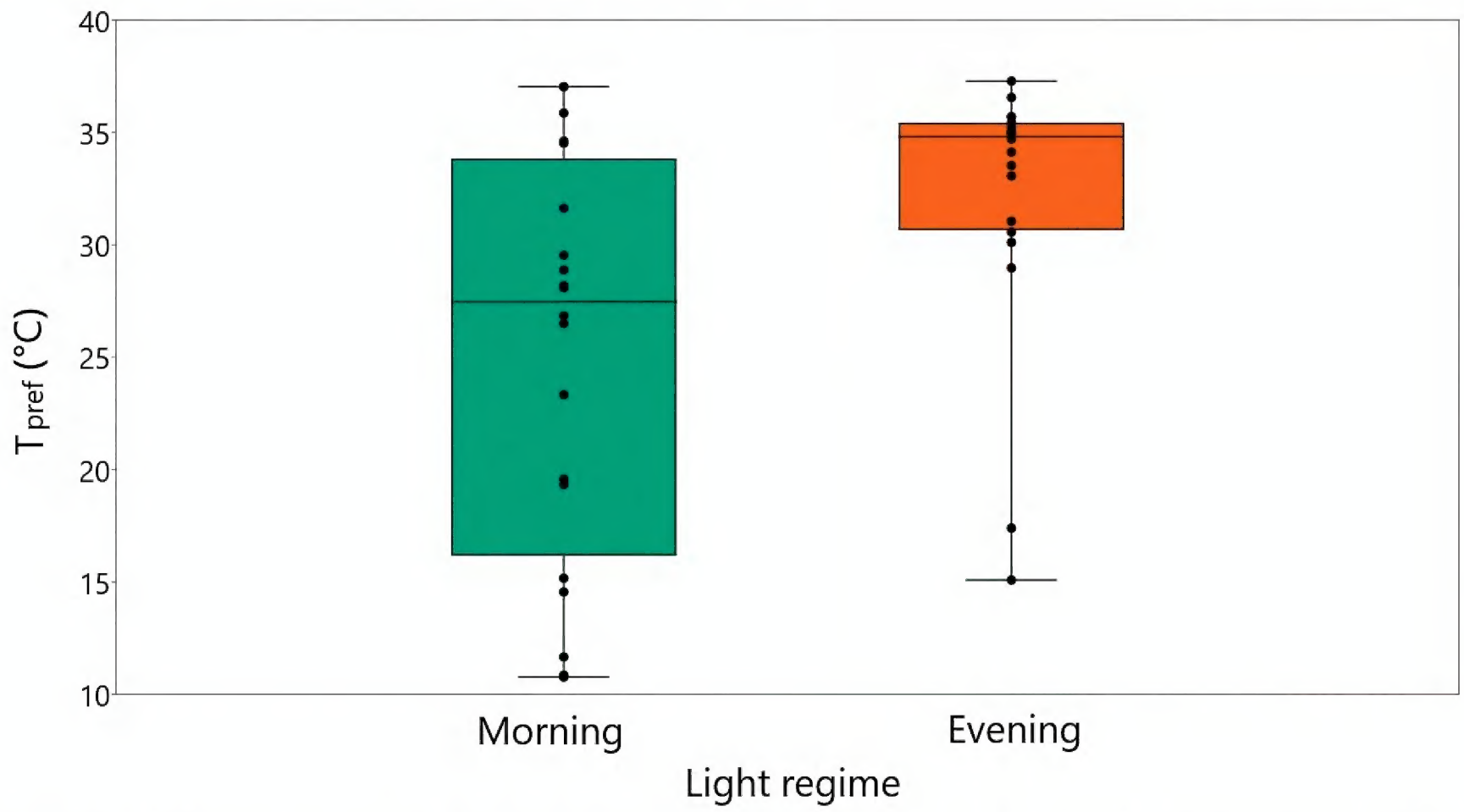


**Figure 4.** Box plot showing preferred body temperature ($T_{pref}$) for *Phyllodactylus gerrhopygus*. The box represents the middle 50% of observed values. $T_{pref}$ was significantly higher during the evening than the morning period.

This pattern is consistent with nocturnal animals living in arid environments (Angilletta et al. 1991; Alfaro et al. 2013; Lara-Resendiz et al. 2013; Taucare-Ríos et al. 2020).

Warm preferred body temperatures selected by geckos may reflect a phylogenetic inertia in the Phyllodactylidae family. In fact, species such as *P. bordai* and *P. gerrhopygus* show similar responses to environmental changes (Lara-Resendiz et al. 2013). Phylogenetic inertia means that these species retain evolutionary adaptations in thermal preferences to variable environments, responding with a similar phenotypic flexibility in both physiological and morphological traits (Labra et al. 2009). Nocturnal geckos tend to select high temperatures in desert environments, showing eurythermic behaviour (Angilletta et al. 1991; Lara-Resendiz et al. 2013; Tan and Schwanz 2015; Cardona-Botero et al. 2019). The study by Lara-Resendiz et al. (2013) in *P. bordai* shows us that thigmothermy and thermoconformity are common strategies in geckos of the genus *Phyllodactylus*. The $T_{pref}$ found in *P. bordai* was 29.9 °C with an interval by $T_{pref}$ (25–75%) of 27.8–32.6 °C, while our results show a $T_{pref}$ of 28.63 °C with an interval by $T_{pref}$ (25–75%) of 25.55–35.7 °C for *P. gerrhopygus*.

Our results show that the $T_{pref}$ is similar to the temperatures found in their microhabitat, indicating that the geckos achieve their preferred temperature by obtaining heat from the environment. This species maintains field

$T_b$ within its $T_{pref}$ range to carry out its temperature-dependent physiological processes, such as digestion and reproduction, which have been found in other nocturnal reptiles (Angilletta and Werner 1998; Angilletta et al. 1999; Aguilar and Cruz 2010; Lara-Resendiz et al. 2013).

On the other hand, we found a significant variation in $T_{pref}$ during the day, a pattern that can be explained by the changes in the activity of these animals (Hays et al. 2019). The upper surfaces of the rocks would be warmer due to an accumulation of heat during sun exposure (Huey et al. 1989; Angilletta et al. 1999). Previous studies have shown that $T_{pref}$ in nocturnal geckos, determined in a laboratory thermal gradient, has been found to range between 25 °C and 35 °C and has been linked to the predatory activity of these animals at night (Dawson 1975; Huey et al. 1989; Angilletta and Werner 1998; Angilletta et al. 1999; Lara-Resendiz et al. 2013; Hays et al. 2019). Additionally, activity at night may facilitate predator avoidance, as many lizard predators (e.g. birds) are either inactive at night or have decreased capacity to see prey (Hays et al. 2019).

Thigmothermic animals exhibit this pattern, as they maintain relatively high temperatures within their shelters during the day to increase metabolic efficiency and, at night, they operate at low or suboptimal body temperatures (Bustard 1967; Avery 1982; Rock and Cree 2008; Lara-Resendiz et al. 2013). Therefore, the bimodality in $T_{pref}$ found in this study would account for a physiological adaptation of nocturnal animals to high daily thermal oscillations (Angilletta et al. 1999; Alfaro et al. 2013; Taucare-Ríos et al. 2020). This same $T_{pref}$ variation has been found in other nocturnal ectotherms (e.g. reptiles and arthropods) from desert climates (Angilletta et al. 1999; Aguilar and Cruz 2010; Lara-Resendiz et al. 2013; Mouadi et al. 2020; Taucare-Ríos et al. 2020).

Refuge temperature and microhabitat selection are fundamental aspects of small ectotherms (Webb and Shine 2000; Goldsbrough et al. 2004). In this case, *P. gerrhopygus* selects warm shelters ($T_s$ = 25.81 ± 5.13 °C; $T_b$ = 26.1 ± 4.05 °C) during the day. This selection of microhabitat could increase locomotion, sprint speed, growth, possibly auditory sensitivity, predation and predatory avoidance (Avery 1982; Huey et al. 1989; Rock and Cree 2008; Aguilar and Cruz 2010; Hays et al. 2019). This species is highly dependent on the $T_s$, employing a thigmothermic strategy similar to that of other Neotropical geckos (Marquet et al. 1990; Aun and Martori 1994; Colli et al. 2003; Aguilar and Cruz 2010; Lara-Resendiz et al. 2013). Some studies suggest that diurnal refuge temperature may stem from the necessity of reaching high enough $T_b$ to complete digestive and physiological processes related to the previous night's activity (Kearney and Predavec 2000; Aguilar and Cruz 2010). Similarly, *P. gerrhopygus* is a thermoconformer species that depends directly on the thermal fluctuations of its environment. These fluctuations would force them to remain hidden in thermally adequate shelters during the day, limiting their thermoregulation capacity. This thermoconformity may enable these animals to conserve time and energy for hunting and feeding, rather than devoting it to thermoregulatory activities (Huey and Slatkin 1976; Labra and Vidal 2003).

Finally, we found that adults and juveniles have similar $T_{pref}$ in laboratory conditions. Previous studies suggest that *P. gerrhopygus* does not exhibit ontogenetic differences in microhabitat use and does not compete for access to suitable rocks (Mella and Reyes 2022). We assume that both juveniles and adults require the exact thermal requirements for their growth and foraging activities. Similar results were found by Angilletta and Werner (1998) and Angilletta et al. (1999) for nocturnal geckos. On the contrary, other studies have found opposite results, where juveniles had a lower $T_{pref}$ than adults (Hitchcock and McBrayer 2006). Future studies should provide more in-depth information on these results, as we are uncertain about the underlying causes of this phenomenon.

In conclusion, *P. gerrhopygus* is an eurythermic species that can select a wide range of temperatures during the day. The $T_{pref}$ increases during the evening as part of its strategy to maximise locomotor activity, prey capture and digestion. This reptile selects thermally favourable shelters that allow it to reach its $T_{pref}$. Our results suggest that this gecko is a thigmothermic and thermoconformer species. Both juveniles and adults choose the same temperatures and may share the same microhabitats. This paper represents the first work on the thermal ecology of this species. Future studies should focus on the effect that climate change could have on this gecko and its distribution.

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# Supplementary material 1

## Thermal preference of *P. gerrhopygus*

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Data type: xlsx

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